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FRUIT SUGAR PREFERENCES OF HOUSE FINCHES

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ABSTRACT.—In a series of choice tests, we determined the relative preferences of House Finches (*Carpodacus mexicanus*) for equicaloric aqueous solutions of hexoses (1:1 mixture of fructose and glucose) and sucrose. At 2% (m/v), birds consumed each sugar solution equally and in amounts similar to plain water. Consumption of hexose but not sucrose increased at 4% sugar concentration. At 6% and 10%, finches displayed consistent, strong preferences for the hexoses over sucrose. In other passerine species, strong hexose preference has been linked to the absence of sucrase, the enzyme needed for digestion of sucrose. Fecal sugar readings from the House Finches, however, indicated approximately equal assimilation of hexose and sucrose, so the hexose preference apparently is not due to sucrase deficiency. Rather, energetics may determine the finches' sugar preferences: hexoses are rapidly processed because the 6-carbon sugars are readily assimilable whereas sucrose must first be hydrolyzed. *Received 22 Jan. 1998, accepted 30 Aug. 1998.*

Physiology imposes major constraints on the digestion of sugars by some fruit-eating birds. These constraints in turn affect species' food selection behavior. Species of Sturnidae (e.g., European Starling, *Sturnus vulgaris*) and Turdidae (e.g., American Robin, *Turdus migratorius*) are unable to digest sucrose because they lack the enzyme sucrase needed to hydrolyze sucrose into 6-carbon sugars, glucose and fructose that can be assimilated (Martínez del Rio and Stevens 1989, Karasov and Levey 1990). Ingestion of high concentrations of sucrose by these species produces osmotic diarrhea and, in extreme cases, death (Martínez del Rio et al. 1988, Brugger and Nelms 1991). Consequently, in feeding and drinking trials starlings and robins learn to avoid sucrose (Schuler 1983, Martínez del Rio et al. 1988, Brugger 1992).

Although Cedar Waxwings (*Bombycilla cedrorum*) can digest sucrose, in choice tests they also prefer hexoses to sucrose (Martínez del Rio et al. 1989, Avery et al. 1995). Waxwings exhibit very rapid gut passage rates (Levey and Grajal 1991). As a result, sucrose is not in the gut long enough to be completely hydrolyzed and is therefore inefficiently assimilated relative to hexose sugars (Martínez del Rio et al. 1989).

In the Icteridae and Emberizidae, two frugivorous species, the Yellow-winged Cacique (*Cacicus melanicterus*) and the Yellow-breasted Chat (*Icteria virens*) preferred 15% (by mass) hexose solution over sucrose solution and displayed relatively inefficient sucrose digestion (Martínez del Rio and Restrepo 1993). Conversely, Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*), granivorous icterids, preferred sucrose solutions to water but did not distinguish between 0.175M and 0.35M hexose solutions and water (Martínez del Rio et al. 1988).

The House Finch (*Carpodacus mexicanus*) is primarily granivorous (Martin et al. 1951) but feeds opportunistically on cultivated fruit (Tobin and DeHaven 1984, Avery et al. 1992). To our knowledge the sugar preferences of House Finches and other Fringillidae have not been evaluated. Responses of House Finches to fruit sugars are pertinent to the development of high-sucrose fruit cultivars for potentially reducing bird damage to fruit crops (Brugger et al. 1993, Darnell et al. 1994). Thus, our objectives were (1) to document House Finch consumption of sucrose and hexose in equicaloric aqueous solutions across a range of sugar concentrations typically found in cultivated fruit and (2) to measure fecal sugar to determine relative digestion of sucrose and hexoses.

METHODS

House Finches were from a captive population maintained at the Florida Field Station of the U.S. Dept. of Agriculture's National Wildlife Research Center in Gainesville, Florida. We maintained birds on a mixed seed diet supplemented three days/week with

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apples and lettuce. Testing occurred during October–November 1995. After testing, birds were returned to their home cages.

We removed birds from communal enclosures (2 × 1.5 × 2.2 m) and placed them into individual, visually isolated test cages (45 cm on a side) in a roofed outdoor aviary. To acclimate the birds, we offered plain water tinted with red food coloring in clear glass tubes (8 mm diameter) 4–5 days before testing. We fixed two tubes, 5 cm apart, to the front of each cage. During acclimation, we measured water consumption after 6 h and 24 h daily to determine baseline fluid intake and to accustom the birds to disturbances.

We prepared test solutions by dissolving 20, 40, 60, or 100 g of sucrose or hexose sugars (Sigma Chemical Company, St. Louis, Missouri) in 1 L of distilled water. The hexose solution contained equal amounts of fructose and glucose. We then conducted separate tests at each of 4 sugar concentrations (m/v): 2%, 4%, 6%, and 10%. Tests lasted 4 days and there were 6 birds/group. One hexose tube and one sucrose tube, 5 cm apart, were available during each test. For each cage, we first randomly determined the position of the sucrose tube and then alternated sucrose and hexose positions daily. We removed maintenance food and water at 08:00 and presented the tubes with sugar solutions from 09:00 until 15:00. Maintenance food and water were then returned to the cages.

We measured the amount of solution missing from each tube to the nearest mm, and then converted to amount of sugar (g) ingested for analyses. We assessed sugar consumption in a 3-way analysis of variance, with sugar concentration as the independent factor, and repeated measures over sugar type and days. We used Tukey's HSD test (Steel and Torrie 1980) to isolate differences ($P < 0.05$) among means.

To determine relative digestion by finches of sucrose and hexoses, we analysed fecal sugar with a hand-held refractometer (Hainesworth 1974, Brugger et al. 1993). We offered six birds a 10% (m/v) agar-sucrose mixture (Avery et al. 1995) for 6 hours and offered similar food made with hexose (equal amounts of glucose and fructose) for 6 hours the next day. We measured three fresh defecations from each bird with each sugar treatment, and compared mean values in a paired *t*-test against a null hypothesis of no difference between sugars. Refractometer readings are expressed as degrees Brix which corresponds to the percentage of sugar present in the sample on a mass : mass basis (Bolten et al. 1979).

RESULTS

Total sugar consumption varied ($F_{1,20} = 22.77$, $P < 0.001$) with concentration. Sugar ingestion at 6% (mean ± SE, $\bar{x} = 1.07 \pm 0.12$ g/bird) and 10% ($\bar{x} = 1.66 \pm 0.11$ g/bird) exceeded that at 2% ($\bar{x} = 0.03 \pm 0.01$ g/bird) and 4% ($\bar{x} = 0.29 \pm 0.08$ g/bird). Overall, hexose consumption (0.67 ± 0.07 g/bird) exceeded ($F_{1,20} = 93.55$, $P < 0.001$) sucrose consumption (0.09 ± 0.02 g/bird). Finches consumed less sugar ($F_{3,60} = 2.83$, $P = 0.046$) on day 1 (0.61 ± 0.17 g/bird) than on days 2–4 (mean consumption 0.79–0.83 g/bird).

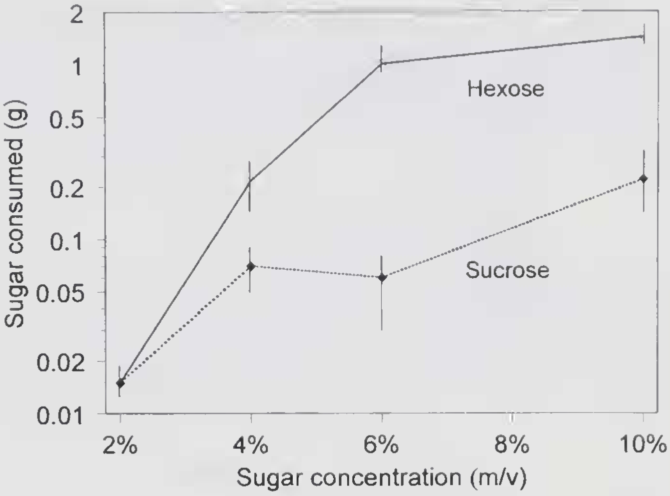

FIG. 1. Mean consumption of hexoses and sucrose by House Finch groups (6 birds/group) exposed to two tubes of aqueous sugar solutions for 4 days, 6 hours per day. Vertical bars denote 1 SE. Note that the y axis is logarithmic.

Across the range of test concentrations, finches responded differently ($F_{3,20} = 24.78$, $P < 0.001$) to the two types of sugars (Fig. 1). Sucrose consumption was consistently low (mean consumption 0.02–0.22 g/bird) and did not differ from hexose consumption at 2% (0.02 ± 0.01 g/bird) and 4% (0.22 ± 0.07 g/bird). Hexose consumption increased ($P < 0.05$) substantially, however, at 6% (1.01 ± 0.11 g/bird) and at 10% (1.43 ± 0.10 g/bird).

The interaction between type of sugar and test day affected consumption ($F_{3,60} = 16.59$, $P < 0.001$). Sucrose consumption did not differ across the 4 test days, and on day 1, mean sucrose consumption (0.22 ± 0.10 g/bird) equalled hexose consumption (0.39 ± 0.10 g/bird). Hexose consumption increased thereafter and averaged 0.73 to 0.79 g/bird on days 2–4.

The 3-way interaction ($F_{9,60} = 5.31$, $P < 0.001$) reflected differing daily consumption patterns of the two sugar types as sugar concentration varied (Fig. 2). At 2%, consumption of both types of sugar remained low throughout the test. At 4%, mean hexose consumption increased each day but not sufficiently to achieve statistical significance ($P > 0.05$). At 6%, mean hexose consumption increased ($P < 0.05$) from day 1 (0.66 ± 0.21

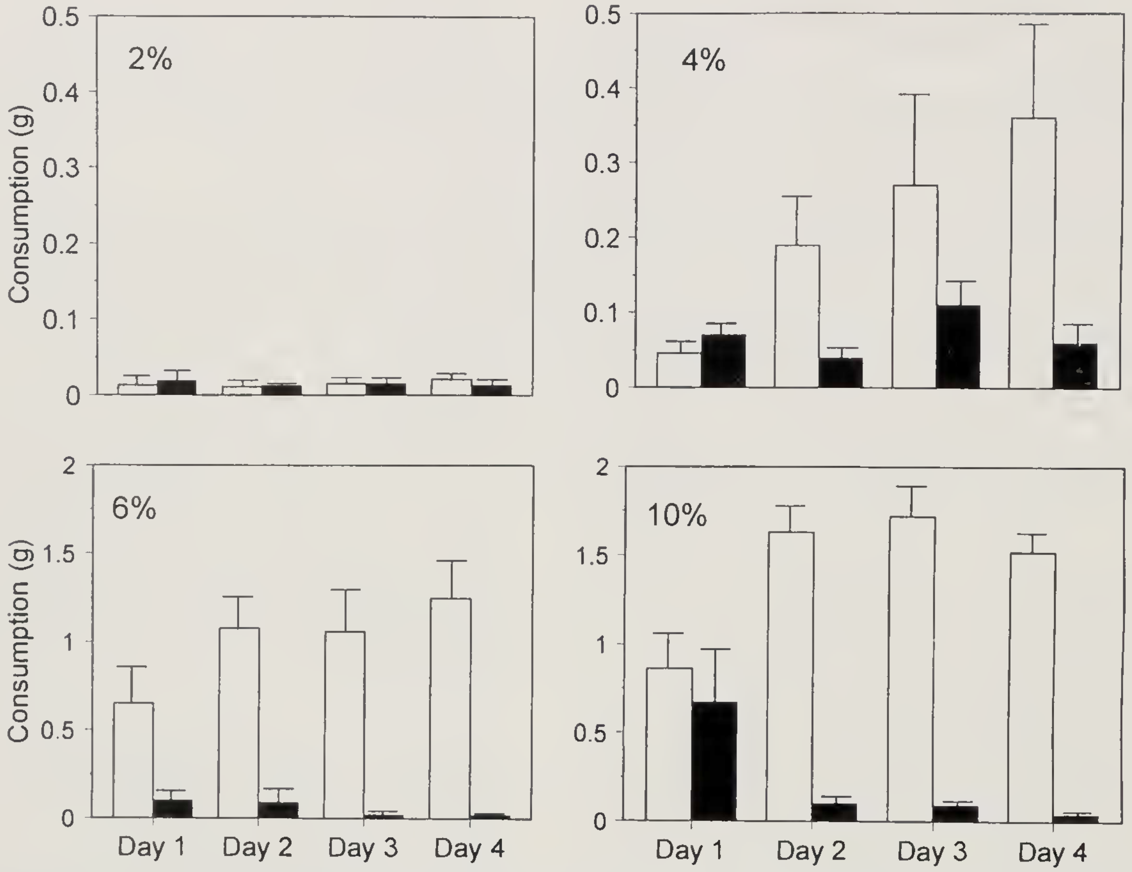

FIG. 2. Mean daily consumption of hexoses (open bars) and sucrose (solid bars) by House Finches (6 birds/trial) exposed to two tubes of aqueous sugar solutions for 6 hours each day. Vertical bars denote 1 SE.

g/bird) to day 4 (1.25 ± 0.22 g/bird). On day 1, finches consumed equal amounts of hexose and sucrose at the 10% level, but consumption diverged ($P < 0.05$) on day 2 and remained so through day 4.

During pretest days, hourly consumption of water averaged 0.22 ± 0.10 and 0.33 ± 0.07 ml/bird for the 2% and 4% groups, respectively, similar to their total consumption of 2% (0.25 ± 0.03 ml/bird) and 4% (1.19 ± 0.30 ml/bird) sugar solutions. Fecal sugar analysis from six birds revealed no difference ($t = 1.63$, $P > 0.05$) between sugars. Hexose readings averaged 4.2 ± 0.7° Brix compared to an average of 2.8 ± 0.3° Brix for sucrose.

DISCUSSION

In the range of concentrations we tested, preference for hexose over sucrose has not previously been demonstrated, even in species lacking sucrase. Rejection of sucrose by European Starlings and American Robins occurred at concentrations in excess of 10% (Schuler 1983, Martínez del Rio et al. 1988, Brugger 1992). Other species are either indifferent (domestic hen, Kare and Medway 1959; Rock Dove, *Columba livia,* Duncan 1960; Common Raven, *Corvus corax,* Harriman and Fry 1990) or prefer sucrose (Common Grackle, Red-winged Blackbird; Martínez del Rio et al. 1988). In choice tests, hummingbirds prefer sucrose and reject fructose (Stiles 1976), but when fructose is offered alone, hummingbirds consume it at a rate no different from sucrose. Other nectarivorous species also select sucrose preferentially over equimolar fructose and glucose solutions (Downs and Perrin 1996).

The sugar solutions we offered appeared alike to us and their relative positions were switched daily. At 2%, it appeared that finches did not distinguish dilute sugar solutions from plain water; consumption was low and remained so throughout the trial. Finches responded to sugar at the 4% level, and mean consumption of hexose increased steadily across the 4-day trial while sucrose consumption remained low. At 6%, hexose consumption increased markedly over that at 2% and 4%, while sucrose consumption did not differ from that at lower concentrations. Discrimination between sugars was more rapid at 10%, as finches decisively selected hexose over sucrose after one trial. The birds apparently tracked the position of the hexose tube through a nonvisual cue. The mechanism by which they discriminated hexose from sucrose is unclear, but the rapidity of the discrimination increased with sugar concentration.

We hypothesize that finches chose hexoses in response to an increased rate of energy gain relative to sucrose solutions during the 6-h drinking trials. Birds are sensitive to differences in rates of energy assimilation (Witmer 1994), and the extra step, hydrolysis of the sucrose molecule required for sucrose digestion imposes a constraint on the potential rate of energy assimilation. In our choice tests, finches responded facultatively and selected the more energetically efficient food source.

Martínez del Rio and coworkers (1988) predicted that granivores should have high sucrase activity and prefer, or at least tolerate, sucrose. This follows from the facts that maltose is the major constituent of complex carbohydrates found in seeds, granivorous species show high intestinal maltase activity, and the activity of sucrase seems to vary with that of maltase and isomaltase (Martínez del Rio 1990, Martínez del Rio et al. 1995). Although House Finches are basically granivorous, they strongly favored moderate hexose sugar solutions over sucrose (Figs. 1, 2). We did not determine intestinal enzyme activity directly, but fecal sugar analyses indicated that the preference for hexoses was not because of absence of sucrase. House Finches prefer hexose sugars but are "sucrose tolerant" granivores, consistent with the hypothesis of Martínez del Rio and coworkers (1988). Comparative studies of House Finches and other granivores will help to define more clearly the physiological basis underlying their food selection behavior.

Development of high-sucrose fruit cultivars could represent one nonlethal component of an integrated plan to manage bird damage to berry crops (Brugger et al. 1993, Darnell et al. 1994). Such an approach will most likely be effective against species such as the European Starling and American Robin that lack sucrase and are thus unable to digest sucrose. For sucrose tolerant species such as the House Finch, elevated sucrose concentrations in fruit will probably not reduce crop damage unless alternative food sources are readily available. Rather, because of inefficient energy assimilation from sucrose ingestion, sucrose tolerant species might compensate by increasing fruit consumption, thereby causing greater damage (Avery et al. 1995).

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